

Prey capture in orb weaving spiders: are we using the best metric?

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Abstract. Orb spiders are commonly used to study many ecological and behavioral questions, due in part to the ease of working with their webs. The frequency distributions of prey captured by spiders are often compared among species or individuals to search for evidence of competition, effects of experimental manipulations, etc. In most instances, smaller insects are extremely common compared to larger prey, presenting a critical flaw in how such comparisons are analyzed because natural selection acts upon web evolution through the biomass, rather than total number, of prey captured. The “rare, large prey” hypothesis, developed for *Zygiella x-notata* (Clerk 1757), suggests that orb spiders derive the bulk of their energy not from common prey, but rather from a small subset of the largest possible insects. If correct, then orb webs should be designed to facilitate the capture of these insects, which are essential for spider fitness, even though they rarely fly into webs. Here, I test the generality of the “rare, large prey” hypothesis by comparing the frequency and biomass of large prey in 38 studies of the diets of 31 species of orb spiders in four different families. I define large prey as insects at least 66% as long as the spiders capturing them. The 38 studies included both large and small species of spiders, living in both tropical and temperate habitats. Large insects accounted for only 17% of the total number of prey captured by spiders, but contributed 85% of the total consumable biomass. The “rare, large prey” hypothesis thus can apparently be generalized across orb spiders. Future experiments need to account for the disproportionate influence of these large insects on spider fitness and on how to effectively measure these rare events. More importantly, the “rare, large prey” hypothesis provides a new framework in which to better understand variation in the web spinning behaviors of spiders.

Keywords: Foraging theory, optimal foraging, rare event, risk sensitivity, spider web

Orb weaving spiders are both important and convenient study systems for many ecological and behavioral questions (Eberhard 1990; Wise 1993; Foelix 1996; Vollrath & Selden 2007). The webs themselves make orb spiders particularly amenable for study. Web architectures capture a variety of behavioral decisions, made by spiders during the establishment and spinning of webs, into physical structures that are easily quantified and manipulated. Yet, there is little consensus on how many features of orb webs influence foraging success and ultimately fitness (Eberhard 1990; Heiling & Herberstein 2000). The number and taxa of prey captured by webs are often compared among sympatric species of spiders to search for evidence of potential niche partitioning (Brown 1981; Horton & Wise 1983; Nyffeler & Sterling 1994) or adaptive radiation (Blackledge et al. 2003). In most instances, differences in the numerical abundances of prey are then used to infer how natural selection has shaped web spinning behaviors. Only rarely is size considered (e.g., Wise & Barata 1983).

However, there is a potentially critical flaw in such comparisons. Natural selection acts upon foraging behaviors only in so much as variation in those behaviors influences the quantity or quality of offspring produced. Fecundity and survival in spiders correlates directly with consumed biomass, but simple comparisons of numbers of prey captured will be very misleading if prey biomass itself does not scale directly with numerical abundance (Miyashita 1992a; Tso and Severinghaus 1998). For instance, an adaptive partitioning of resources might be inferred between two species of spiders if they differ in the frequency of small dipteran prey in their diets, even though both species acquire the bulk of their energy from the same, large prey items. Even when prey sizes are directly measured, comparisons usually are made using parametric statistics, such as mean mass, without considering

the potentially extreme importance of large outliers (Nentwig 1985). Venner and Casas (2005) provided an elegant demonstration of the importance of this perspective for the orb spider *Zygiella x-notata*. They used field data on prey capture and spider growth to show that reproduction depended primarily on the capture of what they termed “rare, large prey”. Subsequently Blackledge and Eliason (2007) tested the role of capture spiral density, or “mesh width”, in *Argiope aurantia* (Fabricius 1775) by removing every other row of the spiral from an experimental group and then comparing the weight gain of these spiders over the course of a single day of foraging to that of control spiders with intact webs. They found no difference in weight gain, suggesting that spiders were spinning “suboptimally large amounts of sticky silk” in webs. Blackledge and Eliason explained this paradox through the presence of large prey – the control group had three times more wrapped prey remaining in webs at the end of the day. These large insects represented half of the total consumable biomass captured by spiders.

But, how general is the importance of exceptionally large insects in spider diets? Prey density and size distribution vary among habitats. Moreover, what constitutes a “large” prey to one spider species versus another depends greatly on interspecific variation in spider body size, which itself ranges over 1.5 orders of magnitude among orb spiders (Blackledge et al. 2009). I test here the generality of the “rare, large prey” hypothesis across many taxa of orb spiders that occur in diverse habitats and vary greatly in absolute spider body. I then discuss some of the implications of the “rare, large prey” hypothesis for how orb webs function and how spinning behaviors evolved. In particular, the design of orb webs should reflect the mechanical challenges presented by larger insects, which may lead to counter-intuitive results. For instance, given equivalent silk resources, smaller orb webs may function

"better" than bigger webs at capturing larger insects if they are spun from thicker, more tightly packed threads. Studies relating variation in web architecture to prey capture must therefore begin to integrate information about silk structure and biomechanics if they are going to succeed in understanding how spiders use orb webs to target specific prey (Harmer et al. 2011).

METHODS

I surveyed all of the reasonably obtainable literature on prey capture by orb weaving spiders published since 1970, primarily utilizing the ISI Web of Science database. I examined all studies that included both quantification of the abundance of different prey taxa and some measure of prey size – either body mass or, more commonly, total body length. My goal was to calculate both the numerical abundance and the total biomass for different size classes of prey. In instances where only prey length was recorded, I used the power relationship:

$$\text{Mass} = 0.022 * \text{Length}^{2.4}$$

to estimate total wet mass of insects from body length, or vice versa for instances where only prey mass was recorded. Many studies provide more precise equations describing how mass and length scale for specific insect taxa in specific habitats (e.g., Rogers et al. 1977; Sample et al. 1993), but the values I use here represent the midrange of parameters for diverse groups of insects estimated by Schoener (1980). I also repeated the analysis with estimated mass scaling as a square and then a cube with body length to assess the effects of extremes in these scaling relationships. I ranked prey by body length using the smallest bins possible for each study. This typically resulted in ~10 size classes of prey, but sometimes as few as three or as many as 29. I compare body lengths between prey and spiders to determine which insects are "large" because studies often cite only the total body lengths of spiders and because length can be a more consistent indicator of spider size.

Spider size was either taken directly from the publication or, if not stated, from the taxonomic literature for that species. I excluded one study with appropriate prey data because it specifically involved immature spiders for which no size data were provided (Endo 1988). All included studies either explicitly focused upon adult female spiders or were assumed to do so because they did not otherwise specify information about spider size or maturity. Focusing on adult females may limit generality to other stages in ontogeny, but there was no a priori reason to believe this, and my approach was consistent with the focus of most studies on spider ecology and behavior. Moreover, the size range among the adult females of different species in this study was comparable to much of the range in body size within any individual species during development.

I then computed the total number and the total biomass of prey that were at least 66% as long as the spider for each study. The choice of prey size equal or greater than 66% of the spider's length was arbitrary, but I also considered other metrics such as the subset of largest prey that constituted 25% of all biomass or the subset of prey that were at least equal to the spider's size. These other metrics gave qualitatively similar results and were therefore not reported. I used nonparametric statistical tests due to the highly skewed distributions of the data.

RESULTS

Spider body length ranged from 5–26mm and included taxa from four families (Araneidae, Nephilidae, Tetragnathidae & Uloboridae). There was a slight bias toward three commonly studied genera (*Argiope* Audouin 1826, *Metepseira* Cambridge 1903, and *Nephila* Leach 1815), but the dataset included 31 species in 18 genera for a total of 38 studies (Table 1).

The frequency of large prey and their contribution to the biomass captured by orb spiders differed significantly (Fig. 1). Large insects accounted for only 16.5% (8–25%, lower and upper quartiles) of the total number of prey captured by spiders, but larger insects contributed more than 84.5% (59–91%, lower and upper quartiles) of the total consumable biomass. Scaling body mass as only the square of body length reduced the contribution of large insects to 76% while scaling body mass as the cube of length increased the contribution of large insects to 86%. Both the overwhelming contribution to biomass by large prey and the relative rarity of large prey were uncorrelated with spider body length (Fig. 2, Spearman Rank Order Correlations at $P < 0.05$).

DISCUSSION

The "rare, large prey" hypothesis presents three challenges for understanding spider orb web function. First, ecologists should take care in how they interpret data from prey capture surveys when most of the data they collect likely has little impact upon spider fitness. Second, researchers need to rethink how to design experiments to best quantify these rare data. Finally, arachnologists should consider how natural selection has shaped orb webs as traps for insects, because the functional implications of evolutionary and behavioral variation in orb web architecture can only be understood by integrating web geometry with knowledge of the structure and biomechanics of silk threads.

Araneoid orb weaving spiders clearly obtain the bulk of their energy from a subset of rare, large prey (Fig. 1). Arbitrarily defined here as insects at least 66% the length of spiders, large prey account for fewer than 17% of all insects captured but contribute 85% of the biomass captured. While not unbiased in focal species, the diversity of studies in this meta-analysis suggests that the "rare, large prey" hypothesis, first explicitly tested by Venner and Casas (2005) and hinted at by earlier studies (e.g., Brown 1981; Miyashita 1992a; Miyashita & Shinkai 1995), is generalizable for most orb weaving spiders. Its importance for other spiders such as cursorial hunting RTA clade species or three-dimensional web builders remains to be tested (but see Fritz and Morse 1985). However, it is plausible given the ability of most spiders to consume exceptionally large insects in single meals (Foelix 1996). While the tremendous diversity of orb weaving spiders and their web spinning behaviors virtually guarantees exceptions, the "rare, large prey" hypothesis presents three important challenges for understanding the foraging behaviors of most orb spiders.

The first challenge involves using prey capture to infer fitness consequences, as is often done by comparing numerical lists of prey captured by different spiders to infer functional differences in orb webs (see reviews in Eberhard 1990; Wise 1993). Such lists are easily compiled and handled statistically, and spider fecundity is clearly limited by food intake (see

Table 1.—Species from which prey data were obtained.

Species	Body length (mm)	Habitat, country	Total number of prey	Source
Araneidae				
<i>Aculepeira ceropegia</i> (Walckenaer 1802)	11.5	Fields, France	58	Pasquet & Leborgne 1990
<i>Agalantaea redii</i> (Scopoli 1763)	7.5	Fields, France	110	Pasquet & Leborgne 1990
<i>Araneus cavaticus</i> (Keyserling 1881)	17.5	Cliffs, USA	n.a.	Riechert & Cady 1983
<i>Araneus diadematus</i> Clerk 1757	9	n.a., England	1432	Walker 1992
<i>Araneus marmoreus</i> Clerk 1757	12	Fields, France	27	Pasquet & Leborgne 1990
<i>Argiope amoena</i> L. Koch 1878	25	Orchard, Japan	387	Murakami 1983
<i>Argiope argentata</i> (Fabricius 1775)	12	Tropical grassland, Panama	3202	Nentwig 1985
<i>Argiope argentata</i>	12	Tropical grassland, Panama	4672	Robinson & Robinson 1970
<i>Argiope aurantia</i> ¹ Lucas 1833	19.5	Grassy field, USA	44	Nyffeler et al. 1987
<i>Argiope aurantia</i> ²	19.5	Cotton field, USA	190	Nyffeler et al. 1987
<i>Argiope aurantia</i>	19.5	Field, USA	270	Blackledge & Wenzel 1999
<i>Argiope bruennichi</i> (Scopoli 1772)	15.5	Field, France	16	Pasquet & Leborgne 1990
<i>Argiope savignyi</i> Levi 1968	10	Tropical grassland, Panama	287	Nentwig 1985
<i>Argiope trifasciata</i> (Forsskål 1775)	17.5	Fields, USA	113	Brown 1981
<i>Cyclosa argenteoalba</i> Bösenberg & Strand 1906	4 ²	Forest, Japan	90	Miyashita 1997
<i>Cyclosa octotuberculata</i> Karsch 1879	4 ²	Forest, Japan	76	Miyashita 1997
<i>Cyclosa sedeculata</i> Karsch 1879	4 ²	Forest, Japan	64	Miyashita 1997
<i>Eriophora fuliginea</i> (C.L. Koch 1838)	22	Tropical forest, Panama	2632	Nentwig 1985
<i>Gasteracantha caneriformis</i> (Linnaeus 1758)	10	Forest, Japan	66	Yoshida 1989a
<i>Larinioides cornutus</i> (Clerk 1757)	10.3	Riparian, Slovakia	705	Prokop 2005
<i>Mecynogea lemiscata</i> (Walckenaer 1841)	8.3	Forest, USA	95	Wise & Barata 1983
<i>Metepeira incrassata</i> F.O. Pickard-Cambridge 1903	7	Plantation, Mexico	617 ³	Uetz 1989
<i>Metepeira incrassata</i>	7	Plantation, Mexico	296 ⁴	Rayor & Uetz 1990
<i>Metepeira labyrinthea</i> (Hentz 1847)	6.3	Forest, USA	95	Wise & Barata 1983
<i>Metepeira spinipes</i> F.O. Pickard-Cambridge 1903	7	Forest/Field, Mexico	93 ³	Uetz 1989
<i>Micrathena gracilis</i> (Walckenaer 1805)	8.5	Forest, USA	118	Uetz & Hartsock 1987
<i>Zygiella x-notata</i> (Clerck 1757)	6.5	Buildings, France	376	Venner & Casas 2005
<i>Zygiella x-notata</i>	4	n.a., England	1232	Walker 1992
Nephilidae				
<i>Nephila clavata</i> L. Koch 1878	25	Forest, Japan	128	Miyashita 1992b
<i>Nephila clavipes</i> ⁵ (Linnaeus 1767)	26	Forest, Mexico	49	Hodge & Uetz 1992
<i>Nephila clavipes</i>	26	Scrubland, USA	147	Higgins 1987
<i>Nephila clavipes</i>	26	Tropical forest, Panama	5443	Nentwig 1985
Tetragnathidae				
<i>Meta reticuloides</i> Yaginuma 1958	7.5	Cliffs, Japan	142	Yoshida 1990
<i>Metelucauge kompsonensis</i> (Bösenberg & Strand 1906)	11.8 ⁶	Riparian, Japan	105	Yoshida 1989b
<i>Metelucauge yunohamensis</i> (Bösenberg & Strand 1906)	9.3 ⁶	Riparian, Japan	25	Yoshida 1989b
<i>Tetragnatha laboriosa</i> Hentz 1850	7.1	Soybean field, USA	72	LeSar & Unzicker 1978
Uloboridae				
<i>Octonoba sybotides</i> ⁷ (Bösenberg & Strand 1906)	7	Botanical garden, Japan	177	Watanabe 2001
<i>Philoponella republican</i> (Simon 1891)	5	Tropical forest, Peru	343	Binford & Rypstra 1992

Superscripts:

¹ Mean lengths of each taxon used;² Only large spider data included;³ Only data from prey impacting the first web were used;⁴ Only data from webs on periphery of colony included;⁵ Only solitary individuals from first year of study included;⁶ Average for range of body lengths given in the study;⁷ Only spiders in the "abundant prey" category included, n. a. = not available in the publication.

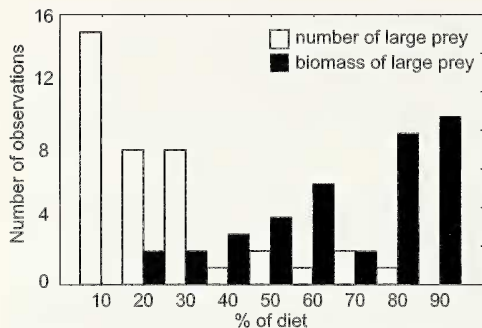


Figure 1.—Comparison of the relative frequency and biomass of larger prey in spider diets ($n = 33$ studies). Large prey are defined as insects at least 66% of the body length of the spider capturing them. Both the number of large insects (white) and the biomass of large insects (black) are presented.

summary in Wise 1993). However, the conclusions from these comparisons can be quite misleading when most of the observed insects are relatively small and contribute very little energy to spiders, because they numerically dominate statistical tests. Studies of how orb webs mediate competition among sympatric species or of adaptive variation in web architecture should instead focus on the prey that ultimately determine variation in spider fitness. Simply put, niche partitioning may not have occurred if two species of spiders differ in the capture of 85% of all insects, but both obtain most of their energy from the same few taxa of rare large prey. Alternatively, including all prey in a statistical analysis might obscure meaningful differences in the types and capture of rare, large prey when such insects are treated as little more than statistical outliers. Finally, manipulating web architecture might not result in detectable differences in the number of prey captured, but still substantially influence the sizes of the very largest prey captured and hence play a major role in determining foraging success (e.g., Blackledge & Eliaison 2007). One potentially critical exception arises if spider fitness

is limited less by prey biomass than by nutrient composition of specific prey (Mayntz & Toft 2001). In such cases small prey may still be critical for fitness despite their minor contribution to biomass. Regardless, simple comparison of prey numbers among orb spiders can clearly mislead.

The generality of the “rare, large prey” hypothesis presents a second major empirical challenge. How do researchers study rare events that they are unlikely to observe over the short time-frames of most field studies? Numbers of prey capture events in this meta-analysis ranged from 16–5443 (median = 128) and roughly correlated with the amount of time spent observing spiders. The lowest and the highest values for both metrics of prey capture (frequency and biomass) occurred in studies within the lowest third of sampling effort. Indeed, large prey were numerically common (> 50% of events) only in three studies, all of which were among the “lowest sampled”. The stochasticity of the capture of rare, large prey means that they are likely difficult or impossible to study in experiments with low sampling effort. Ideally, researchers should increase their sampling efforts in the field and consider applying resampling techniques designed to assess the importance of unobserved rare events, similar to those employed in studies of species richness and biodiversity (e.g., Colwell & Coddington 1994; Scharif et al. 2003), to determine the amount of sampling effort necessary to accurately characterize spider diets.

Finally, arachnologists debate the role of web architecture in determining prey selectivity of orb spiders (e.g., Nentwig 1983; Eberhard 1986; Herberstein & Heiling 1998; Blackledge & Eliaison 2007). Much of this theory rests on the assumption that all, or at least most, prey captured by spiders are of relatively equivalent value for fitness. However, the “rare, large prey” hypothesis argues that natural selection places a premium on the capacity for webs to facilitate the capture of relatively large, rather than abundant, insects. One could argue that the pattern of data presented here might result solely from skew in the size and abundance distribution of insects in the environment. However, this could only be true if orb webs have not been shaped by natural selection for their prey capture function. Moreover, orb webs do not act as passive filters of insects, sampling prey in direct proportion to their abundance in the environment, as refuted by many

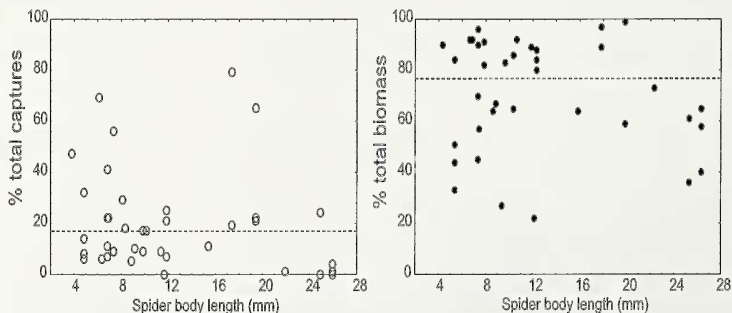


Figure 2.—Variation in the frequency and relative biomass of large insect prey for spiders of different sizes. Large prey are defined as insects at least 66% of the body length of the spider capturing them. The dashed lines indicate the medians.

comparisons of insect availability to their abundance in spider diets (e.g., Nentwig 1983; Nentwig 1985; Walker 1992; Blackledge et al. 2003). Instead, the design of spider orb webs should reflect, in part, selectivity for larger insects. Thus, the potential fitness consequences of variation in orb web architecture can only be interpreted by considering how webs function in the capture of this very challenging subset of prey. Moreover, those fitness consequences can be neither intuited nor tested without also considering variation in the structural, and potentially even material, properties of silk threads. For instance, female gigantism occurs commonly among orb spiders (Hormiga et al. 2000). Evolution of increased body size is repeatedly associated with both behavioral shifts in web spinning and changes in silk biomechanics that improve the stopping potential of these webs compared to smaller species (Agnarsson & Blackledge 2009; Sensenig et al. 2010). This concerted pattern of coevolution between behaviors and biomechanics suggests that capture of large prey becomes increasingly difficult as spider body size evolves larger.

I conclude with one hypothetical example with clear relevance to the growing interest in the literature on intra-individual behavioral and biomaterial plasticity during web spinning (e.g., (Sherman 1994; Heiling & Herberstein 2000; Tso et al. 2005; Tso et al. 2007; Boutry & Blackledge 2008). Does a bigger web indicate increased foraging effort? Many studies suggest yes, arguing that larger capture areas or longer lengths of threads result in higher rates of prey capture (Eberhard 1986; Sherman 1994; Venner & Casas 2005), at least up to some upper limit (Higgins and Buskirk 1992). Clearly, if a spider builds a smaller web, then that web should intercept fewer insects compared to a bigger web, but that smaller web could ultimately result in more biomass of prey for the web owner if spun from thicker or more tightly packed silk threads that more effectively stop and retain larger insects, especially if these properties do not change linearly with variation in web geometry (e.g., Blackledge & Eliason 2007). Thus, by one metric, number of total prey, spreading silk resources into larger webs is better, while a second metric, total biomass, suggests the opposite. In general, the later metric is more likely to play a decisive role in determining fitness.

Alternatively, neither web type might be “best”. The closer relevance of prey biomass to spider fitness suggests that smaller webs are better, so why would spiders increase web size? First, in situations where large prey are easily captured and abundant (such as emergences of weakly flying mayflies or reproductive termites), then biomass intake may be determined more by the number of insects flying into a web than by variation in how effectively the web can dissipate their flight energy (Sandoval 1994). Second, the value of common, low biomass prey for fitness should change with the physiological status of web builders. Energetically stressed spiders, nearer starvation, gain the most fitness from smaller, easily captured insects that might provide just enough biomass to prevent starvation (Venner and Casas 2005). Such spiders therefore benefit more from spinning webs that maximize capture of smaller prey by focusing more on increasing the interception potentials of webs. In contrast, sated spiders gain little fitness from such prey and can instead afford to spin webs that are superior at capturing large prey through increased stopping power, even if their rarity nets the web owner very few

interceptions (see also Miyashita 1992a). Thus, the “rare, large prey” hypothesis also provides a framework to better understand plasticity in the web spinning behaviors of spiders.

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